Reproductive Behaviour of the Indian Spike-tailed Paradise Fish, *Macropodus cupanus* (Cuv. & Val.)[1]

BY

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(*With two plates and a text-figure*)

INTRODUCTION

This paper presents descriptive and quantitative data on the sexual behaviour of the Indian spike-tailed paradise fish, *Macropodus cupanus*, in laboratory aquaria. The life history and early development of *M. cupanus* has been described by Raj (1916), Norman (1936), Jones (1940), and Padmanabhan (1955). No detailed quantitative data are available, however, on the reproductive behaviour of this species.

M. cupanus is an anabantid fish occurring naturally along the Malabar and Coromandel coasts of south India. According to Hervey & Hems (1963), it also occurs in Ceylon, Malay peninsula, and Sumatra. It is a small fish, adults reaching a maximum length of about 6 cm. Males are slightly larger than females. They occur in all types of freshwater : tanks, lakes, ditches, and streams, even in slightly brackish water. Their most typical habitats are wet rice paddy-fields and village tanks or ponds. They are capable of living in foul waters which are deficient in oxygen. They frequent thick vegetation or hide under stones or in crevices along pond edges. They are perennial breeders and the males build ' bubble nests '. They are carnivorous feeders and are considered valuable mosquito larvivores (Jones 1940).

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Materials and Methods

The fish used in this study were wild-trapped in south India and were obtained through a Calcutta tropical fish dealer. When brought to the laboratory most of them were immature, in the size range of 2 to 4 cm. The fishes were fed with dry powdered daphnia and dry 'TRADIS' fish food twice a day and with live tubifex worms once a day. *Vallisnaria spiralis* (domestic variety) was planted in all the breeding tanks. The tanks were lighted with 25 watt electric bulbs from 9 a.m. to 5 p.m. Overhead lights were kept on during working hours. The water temperature of the tanks was kept between 75° F. and 85° F. Most of the tanks used for observing reproductive behaviour were of 2.5 gallon capacity (measuring 30×20×20 cm.). Seven-gallon tanks (46×25×25 cm.) were used as general holding and maturing tanks. The tanks were cleaned twice a week. The fish compositions of the tanks were intentionally varied. Sometimes a mature male was first introduced in the tank and one or two mature females were added afterwards before or after completion of the nest by the male. Sometimes a single mature pair was introduced in the tank together.

Fifty matings have been observed, and precise data have been recorded on 44 of them. This includes data on total duration of mating time, total number of eggs, number and duration of enfoldings[1] (copulations), number of eggs released per enfolding, and interval between enfoldings for each mating. The 44 matings studied in detail included 2128 separate enfoldings.

Results

In this discussion reproductive behaviour of the fish will be considered under 3 headings : Pre-mating, Mating, and Post-mating Behaviour.

PRE-MATING BEHAVIOUR

This period extends from the beginning of courtship display between male and female and ends just before enfolding occurs.

Nest building by the male

M. cupanus males, like all other bubble nest building anabantids, build a bubble nest at the water surface which consists of very small bubbles heaped together. In our laboratory tanks, most of the nests were built at one corner of the tank and in few cases included floating leaf blades. Nest building indicates physiological maturity of the male (Goodrich

[1] The term 'enfolding' is used rather than 'copulation' for two reasons : (1) to agree with the terminology of Forselius (1957), and (2) because fertilization is external.

& Taylor 1934). The males usually take 1½ to 2 hours to build a nest of about 4 cm. diameter and maximum height of 1 cm. The mechanism of building a nest involved the fish taking air in its mouth from the water surface, mixing it with mucus to form a froth, and then blowing several small bubbles which adhere together. This process is repeated many times and gradually a nest takes shape. Nest building is hastened in the presence of a mature female, and also by increased water temperature (Forselius 1957). The nests observed in our laboratory tanks were much smaller than those observed by Jones (1940) and Padmanabhan (1955) in the paddy-fields, which measured about 8 cm. to 13 cm. in diameter and 4 cm. in height.

Male responses towards the female

After completing the nest the male makes short trips to different parts of the tank apparently looking for a female, and returns to the nest quickly. If the male does not find a female for a long time, he does not take care of the nest and the nest breaks down.

When a mature female is in the tank the male will swim towards her and will butt her on the abdomen and on the fins with his snout. He will then swim back to the nest. He may on occasions stop on the way and look back as if to see whether the female is following him. This behaviour has been described for the genus *Macropodus* in general by Forselius (1957), and has been called ' leading to nest ' movement of the male. At this time the male displays erected fins, especially the tail fin. If the female is receptive she will follow the male but if the female is not receptive she will ignore him. Under this circumstance the male becomes aggressive towards the female and will usually chase and bite her.

Males without any nest are to some extent indifferent to immature females but will follow, rub, and butt a receptive female on the abdomen with the snout.

During sexual excitement the body colour of the male turns slightly dark, eyes and pelvic fins become red to orange, and the black spot at the base of the tail fin disappears.

Female responses towards the male

An immature female is usually indifferent to males either with or without nest. An incompletely mature female may start courtship displays with a male with nest. A mature female, when meeting a male without a nest, behaves peculiarly—she waves her body and moves randomly away from the male (sometimes facing the glass of the aquarium). It appears to be an expression of behavioural uncertainty. When a receptive female meets a male with nest she suddenly assumes a dull dark colour, her eyes become dark, the spines of the pelvic fins become orange, and the black spot at the base of the tail fin disappears and turns white. All of these changes occur in approximately 10 seconds.

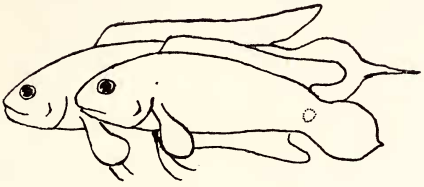
When both individuals are mature either sex can take the initiative for mating. Usually the sex whose reproductive ' tempo '[1] is higher takes the initiative to breed (Forselius 1957). If the female reproductive ' tempo ' is higher than that of the male she will proceed to the male under the nest and start waving her body in a head-down posture at an oblique plane. The male then starts circling movements around her body. Occasionally the female may exhibit head-down posture and body-waving movement at a lower level of water. Sometimes the female may rise up to the water surface at a distance from the nest and, after taking air from the surface, swim directly under the nest in an arc and display head-down, body-waving posture under the nest.

If these displays occur outside the nest the male makes a few circling movements around the female and then swims to the nest. The female normally follows him. Now the sexes engage themselves in circling movements under the nest. They move side by side in two circles—the female in the inner circle and the male in the outer circle moving in the same direction. There may be side dashes between the circling pair but not as vigorous as would be expected in an aggressive encounter. All circling movements do not lead to enfolding. The female after initial circling may settle down on the gravel and remain quiet for 5 to 10 minutes. At this time the male swims over to her and rubs her on the abdomen with the snout and shortly returns back to the nest. After 5 to 10 minutes the female responds to one of these ' leading to nest ' movements of the male and goes to the nest. The circling movements then start again.

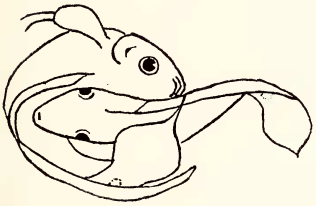
MATING BEHAVIOUR

Before actual enfolding the male and the female move in circles in the same direction. Sometimes the male moves faster and this brings the female's head region to the middle of the male's body. The position is then appropriate for enfolding. Simultaneously the male bends his body in the mid-region, the female begins a partial rotation to a lateral position in the water, and the male slides around to the ventral side of the female. The anterior portion of the female including her vent is then enfolded by the male's body. At this time the male's head and tail fin may touch on the dorsal side of the female. The female then rotates further and is turned upside down (Plate I). The pair usually remain in that posture throughout the duration of the enfolding. Sometimes the female is kept flat on her side at the time of enfolding. The postures of enfolding are basically similar in many species of anabantids. They are

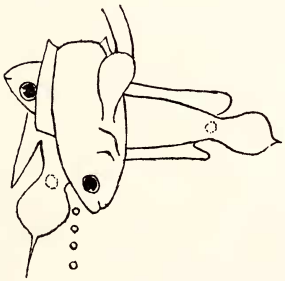
[1] ' Tempo ' is a term used by Aronson (1949) in a way comparable to the psychological terms ' drive ' or ' arousal '.



Circling
(male in background)

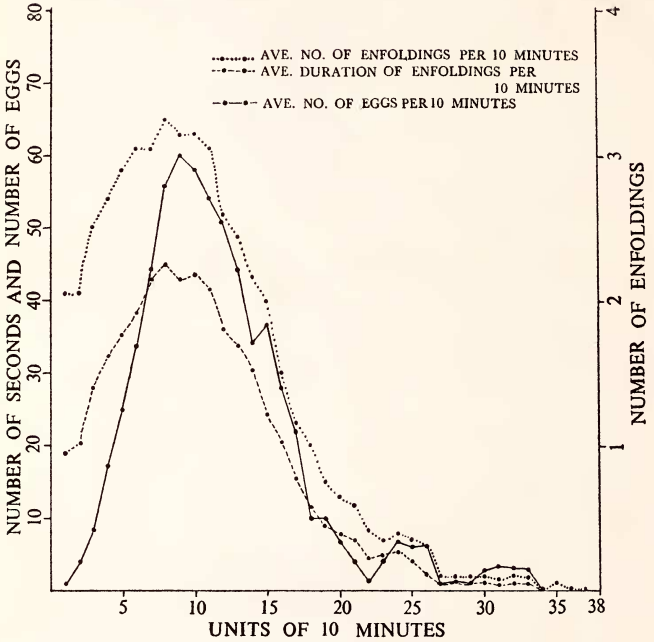


Beginning of enfolding
(female rotates on side, male folds around antero-ventral portion of female)



Enfolding and spawning
(female upside down, male arched dorsally over female as eggs emerge)

Mating postures in *Macropodus cupanus*



Mating pattern of *Macropodus cupanus* in terms of 10-minute units. Based upon averages of 44 matings.

TABLE

REPRODUCTIVE BEHAVIOUR OF *Macropodus cupanus*

MONTH	No. of observed matings	Mean no. of enfoldings per mating	Mean length of mating (Minutes)	Mean total no. of eggs	Mean total length of actual enfoldings (Seconds)	Av. no. of eggs per enfolding	Av. length of enfolding (Seconds)	Av. interval between enfoldings (Minutes)
NOVEMBER 1964	21	56·7 ± 3·7	195·2 ± 13·2	698·9 ± 30·4	750·0 ± 54·2	13·0 ± 0·8	13·1 ± 0·5	3·4 ± 0·2
DECEMBER 1964	12	41·3 ± 3·3	151·7 ± 15·7	608·8 ± 44·0	538·9 ± 46·32	15·2 ± 1·1	13·3 ± 0·4	3·9 ± 0·02
JANUARY 1965	11	40·1 ± 2·6	140·0 ± 13·1	588·2 ± 34·10	463·8 ± 38·56	14·9 ± 0·8	11·5 ± 0·5	3·2 ± 0·02
TOTAL	44	48·4 ± 3·1	169·5 ± 9·0	646·7 ± 21·6	620·9 ± 35·5	14·1 ± 0·5	12·8 ± 0·4	3·4 ± 0·01

accurately portrayed for *Macropodus opercularis* by Innes (1956) and for *Colisa lalia* by Forselius (1957) and these are very similar to *M. cupanus*. The duration of enfolding in *M. cupanus* varied from 5 to 22 sec. with an average of 12·8 seconds (Table). Enfoldings occurred at an average interval of 3·4 minutes.

Sometimes in the circling movement the female moves faster and the head region of the male is at the tail region of the female. Now, while the male continues to move, the female stops, so that the mid-body region of the male comes to the head region of the female and enfolding occurs as usual.

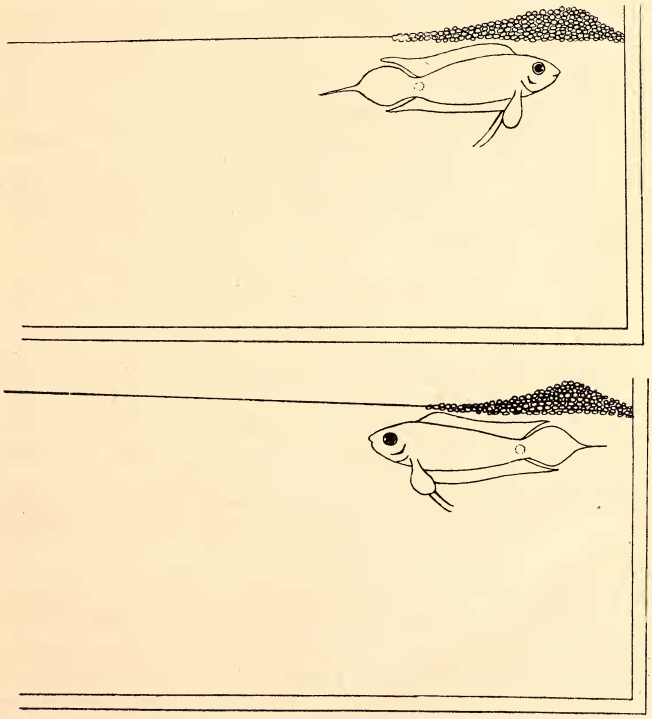
In the enfolded condition, there is no fin movement of the pair. The male's anal fin is curved inward and the female's body takes the form of a shallow ' S '. After a couple of seconds the grip of the male is slightly relaxed. The pair usually float in the enfolded condition but at the beginning of mating, in the first few enfoldings, they sink slowly downwards in the enfolded position. The eggs emerge from the cloaca at the anterior end of the base of the anal fin. The release of eggs and spermatozoa usually occurs within the first 6-8 seconds of enfolding. The number of enfoldings per mating varied from 26 to 102, with an average of 48·4 (Table). The duration of total mating was usually between 2 to 5 hours, and averaged 169·5 minutes. Spawning took place during day-time and more precisely between 11 a.m. to 3 p.m. In the first several enfoldings no eggs are extruded, then the number of eggs gradually increases reaching a maximum in the first half of the mating. Thereafter there is a gradual decrease in the number of eggs until no more are extruded (Plate II). An average of 14·1 eggs were extruded per enfolding with a total average of 646·7 eggs per mating (Table).

After extrusion, the eggs sink slowly in the water and both the parents pick them up into the mouth. The eggs are mixed with mucus and ' blown ' upwards into the bubble nest. The male is more active than the female in picking up the eggs. Usually the eggs at lower levels of water are picked up first and hence very few eggs drop to the bottom. When no more eggs are extruded, the pair still carry on enfolding for several times and then the male suddenly chases and drives the female out of the nest territory. The female does not leave the nest readily and on occasions a fight may occur between the pair. The female is always driven out of the nest territory, however, and she is chased into a corner of the tank away from the nest. By this time the female regains her normal colour. The female from time to time continues to swim up to the nest hesitantly, but is driven off by the male.

The Table at p. 467 indicates a seasonal influence upon the length and productivity of mating behaviour. There was reduced fecundity in December and January in comparison with November. Mating in November with a mean mid-morning temperature of 80·1° F. averaged

56·7 enfoldings per mating, an average mating time of 195·2 minutes, and a total average egg production of 698·9 eggs per mating. December and January, with mean mid-morning temperature of 75·5° F. and 75·8° F. respectively, showed reductions in the number of enfoldings per mating (to 41·3 and 40·1 respectively), the length of mating time (to 151·7 and 140 minutes respectively), and the egg production per mating (to 608·7 and 588·2 respectively). There were no significant monthly differences in the average eggs per enfolding, the average length of enfolding, and the average interval between enfoldings. The latter figures seem to be fairly constant (3·4, 3·9, 3·2) with a very small standard error for the over-all mean ($3{\cdot}38 \pm 0{\cdot}01$).

Our data cannot determine whether these monthly changes in the length and productivity of mating are primarily due to temperature changes, day length changes, or some other factor.



Text-figure. Male in nest guarding postures

POST-MATING BEHAVIOUR

After driving the female away from the nest the male engages in protecting the nest and the brood. He adds new bubbles, re-arranges

the eggs and chases off intruders. While guarding the nest, the male usually faces the corner of the tank and his tail may extend beyond the perimeter of the nest. At this time all the fins of the males are fully extended. Sometimes the male takes a reverse position under the nest, i.e. he faces outwards and his posterior end lies beneath the nest. The male increases the nest area by blowing more bubbles.

Hesitant intruders are immediately chased off by the male as in *Badis badis* (Barlow 1962). But when the intruders come to the nest without stopping the male becomes alarmed and blocks the intruders' way to the nest by placing his body in their path of movement. Then a fight occurs and the intruder is driven away. In every instance observed, the male was dominant in his own nest territory.

The embryos hatch approximately 32 hours after the eggs are laid. The newly hatched larvae cling to the nest in a vertical plane. Larvae which move out of the nest or drop from it are immediately picked up by the male in his mouth and put back to the nest. As the larvae grow older, they move about more freely and are picked up by the male as usual. When the young fry are 3 to 4 days old, they swim about rather freely, and at this stage they are usually eaten by the male, if he is not removed. Padmanabhan (1955) stated that males leave the nest in search of food when the larvae are 3 days old—this possibly occurs in natural conditions and not in laboratory aquaria. We have noticed that while guarding the nest the male takes no interest in the food supplied for 2 to 4 days after hatching.

Discussion

Breeding Season

Thomas (1870) stated that *Macropodus cupanus* breeds during May and June. Jones (1940) collected eggs in January, February, May, September, October, and November and supposed that the fish may be perennial breeders. Padmanabhan (1955) also felt that *M. cupanus* breeds throughout the year. We are in accord with Jones and Padmanabhan and have observed mating in unheated aquaria throughout the winter months in Calcutta from October 1964 to March 1965.

Mating Behaviour

Courtship behaviour is an expression of the level of sexual excitability of the individual and it represents a co-ordination of behavioural activities and physiological processes of both sexes so that a well-synchronized spawning results. In general, the mating behaviour of *M. cupanus* is similar to that of *M. opercularis*, *Colisa* sp., *Trichogaster*, and several other anabantid fishes. The following discussion will consider some specific similarities and differences between *M. cupanus* and other fish.

At mating time most anabantids exhibit colour changes in both sexes. In *M. cupanus*, the males assume slightly dark colour and the females become completely dark including the eyes. Darkening of the eyes during sexual excitement is also seen in *Lebistes reticulatus* (Baerends, Brouwer, & Waterbolk 1955).

In the green sunfish, *Apomotis cyanellus*, the eyes turn black when the fish loses an aggressive encounter (Greenberg 1947). In the climbing perch, *Anabas testudineus*, males turn deep black during sexual excitement (Mookerjee & Mazumder 1946). In *M. opercularis* there is expansion of melanophores on the ventral and lateral sides in both sexes, and colours darken or become more intense (Forselius 1957).

Fishes of the genera *Colisa*, *Betta*, *Macropodus*, and *Trichogaster* are well-known bubble nest builders amongst the anabantid fishes but nest materials often vary. *Macropodus cupanus* males depend on mucus bubbles, anchored to floating vegetable materials like *Pistia*, *Sylvinia*, and *Lemora* plants and have never been found to collect sand grains, detritus, faeces, etc. from the bottom as in *Colisa lalia* and *Trichogaster leeri* (Forselius 1957). Although mating and spawning usually take place after the completion of the nest by the male, mating and nest building in *M. cupanus* may go on simultaneously. Occurrence of spawning in the absence of a nest has also been reported in *C. lalia*, *C. labiosa*, *Osphronemus goramy*, *T. leeri*, and *T. trichopterus* (Forselius 1957). After completion of the nest, the males of most anabantids remain motionless under the nest facing outwards. This has been termed by Forselius as ' nest posting ' of the male. Nest posting of the male has also been observed in *Colisa* and *Trichogaster*. *Badis badis* males remain motionless at the entrance of their burrows (nests) (Barlow 1962).

The leading to nest movement in *M. cupanus* males is similar to that of *C. lalia*, *C. labiosa*, *T. leeri*, and *M. opercularis*. *Betta* males show semi-erected fins while leading the female to the nest. *Badis badis* males on the other hand settle down under the nest at the sight of a receptive female. If *M. cupanus* males fail to conduct the female to the nest, some will nevertheless persist and eventually succeed. Tinbergen (1953) called this ' persuasion '. Persuasion has also been reported in *C. lalia* (Forselius 1957). Many males, however, instead of exhibiting persuasion become aggressive towards the females which do not respond to leading. Aggressiveness of males under this circumstance has been reported by Forselius (1957) in *C. lalia*, *T. leeri*, and *T. trichopterus* and by Barlow (1962) in *Badis badis*. We have not observed males leading the female to non-existing nests, as reported for *Pygosteus pungitius* by Morris (1952). Leading to the nest movement has been described in sunfishes by Breder (1936) but he did not mention the manner of leading. While approaching males under the nest, females of *M. cupanus*, like

those of *T. leeri*, *M. opercularis*, and *C. fasciata*, swim with head pointed downwards.

When mating has actually begun, each successful enfolding seems to stimulate the male to chase off intruders. Enfoldings in which no eggs are released and no (?) ejection of sperm occurs have been termed by Forselius as ' pseudo-spawning '. Pseudo-spawnings occur several times at the beginning and end of mating.

The upside down posture of the female also occurs in *C. lalia*, *Betta splendens*, and *M. opercularis* but is lacking in *C. fasciata*. *Betta* males take the form of an inverted ' U ' while enfolding. Padmanabhan (1955) stated that spawning in *M. cupanus* occurs only in day-time. We agree with this and have observed that most matings take place between 11 a.m. and 3 p.m. In contrast, most of the matings in *A. testudineus* occurred at night (Mookerjee & Mazumder 1946).

A complete mating cycle in *M. cupanus* lasts from 2 to 5 hours which is a wider range than that stated by Padmanabhan (1955). The number of eggs released in each enfolding averaged 14·1 with variation from 1 to 65 (Table). This is similar to egg production in *C. lalia*, *C. labiosa*, and *C. fasciata*. Jones (1940) stated that the eggs are shot up towards the nest by the force of ejaculation and they float with other eggs. Norman (1936) stated that the eggs are light and they float upwards as a result of buoyancy and not through any intervention by the parents. Padmanabhan (1955) stated that the eggs are picked up only by the male and blown upwards into the nest. But we have observed that the eggs sink and are picked up by both the parents and blown into the nest. Mookerjee & Mazumder (1946) stated that the eggs of *A. testudineus* are shot up by the force of ejaculation and float on the surface.

Duration of enfolding averaged 12·8 seconds with variations from 6 to 22 seconds, which is similar to that of Jones's (1940) observation. Jones (1940) stated that the number of eggs laid by a female is about 300. This was supported by Forselius (1957). Padmanabhan stated that on an average 400 eggs are laid by a female but we observed an average of 646·7 eggs per mating, with variation from 299 to 973 (Table).

The interval between 13 successive spawnings of 7 females averaged 14 days with variation from 7 to 25 days. This agrees with Padmanabhan's (1955) findings of 12 to 15 days.

After the termination of oviposition the male spontaneously becomes aggressive to the female and chases her away from the nest. Most previous workers including Jones (1940), Padmanabhan (1955), and Innes (1956) stated that if the female is not removed from the tank after the termination of spawning she is in most cases killed by the male. Our observations in laboratory aquaria showed that the female is not killed. Forselius (1957) reported that males and females of *C. lalia* and *Betta splendens* can be kept together without much injury. We kept and bred